THE UNIVERSITY OF CHICAGO.

FOUNDED BY JOHN D. ROCKEFELLER

The Periodic And Irregular Variations In The Venous Blood-Flow,

A Dissertation submitted to the Faculties of the Graduate Schools of Arts, Literature and Science in candidacy for the degree of Doctor of Philosophy.

DEPARTMENT OF PHYSIOLOGY,

By

RUSSELL BURTON-OPITZ, M. D.

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THE PERIODIC AND IRREGULAR VARIATIONS IN THE VENOUS BLOOD-FLOW

A DISSERTATION

SUBMITTED TO THE FACULTY OF THE OGDEN GRADUATE SCHOOL OF SCIENCE, IN CANDIDACY FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

(DEPARTMENT OF PHYSIOLOGY)

BY
RUSSELL BURTON-OPITZ

CHICAGO
1904

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Reprinted from the American Journal of Physiology.
VOL. VII. — SEPTEMBER 1, 1902. — NO. VI.

THE FLOW OF THE BLOOD IN THE EXTERNAL JUGULAR VEIN.

BY R. BURTON-OPITZ.

[*From the Physiological Laboratory of the Harvard Medical School.*]

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METHOD.

THE blood-flow through the external jugular vein was measured in this investigation with the recording stromuhr devised by Hürthle and demonstrated by him to the members of the last physiological congress, held at Turin, September, 1901.

The stromuhr previously constructed by Hürthle contained two metal revolving cylinders. This new instrument consists of only one cylinder (*C*, Fig. 1) which is stationary and in which a piston (*P*) moves in the vertical direction. The blood reaches the cylinder through the peripheral cannula (*A*) and leaves it through the central cannula (*B*). In its course it passes through a disc (*D*) pierced with two openings. Through one of these the blood enters the cylinder at *E*, below the piston, while through the other it enters a curved tube which conveys it into the cylinder at *E'*, above the piston. At the beginning of the experiment the blood is admitted through *E* and forces the piston to the top of the cylinder. As the piston rises the contents of the cylinder (normal saline solution) are driven through *E'* into the outflow cannula *B*. When the cylinder is full, the perforated disc *D* is turned. The blood now flows from the inflow cannula, *A*, through *E'* into the top of the cylinder. The piston is driven downwards and the contents of the cylinder are forced out through *E* and the outflow cannula *B*.

The piston rod (*T*) is attached to a horizontal writing lever (*L*) by means of a long silk thread. When the piston is driven downward the writing-point of the lever moves upward, and when the piston moves upward, the writing-point moves downward. In Fig. 2 the lever has written two downward phases (*A* to *B* and *E* to *F*) and one upward phase (*C* to *D*). The reversal of the blood-stream by turning the disc has occurred between *B* and *C* and again between *D* and *E*.

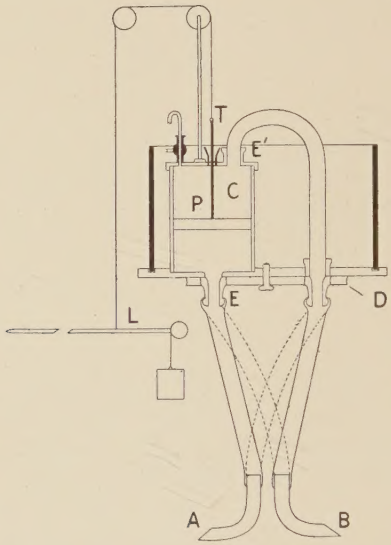

FIGURE 1.—Diagram of Hürthle's Recording Stromuhr.[1] *A* and *B*. Central and peripheral cannulas. *C*. Stationary cylinder. *D*. Revolving disc. *E* and *E'*. Openings in cylinder for entrance of blood. *L*. Writing lever with weight. *P*. Piston. *T*. Tip of piston, connected with lever by means of silk thread.

The cylinder being calibrated, every rise or fall of the lever indicates that a definite quantity of blood has entered or left the stromuhr. In the case illustrated by Fig. 2 a rise of 4 mm. shows that 1 c.c. of blood has entered the instrument. The time, absolutely essential in calculating the results, was recorded by a Jaquet chronometer, beating fifths of seconds. The time record served also as the abscissa for the curve of the blood-flow. The venous pulse and the respiratory movements were also recorded when the occasion demanded.

[1] TSCHUEWSKY, F. A.: О Кровоснабженіи Отдѣльныхъ Органовъ (On the blood-supply of several organs), Charkow, 1902.

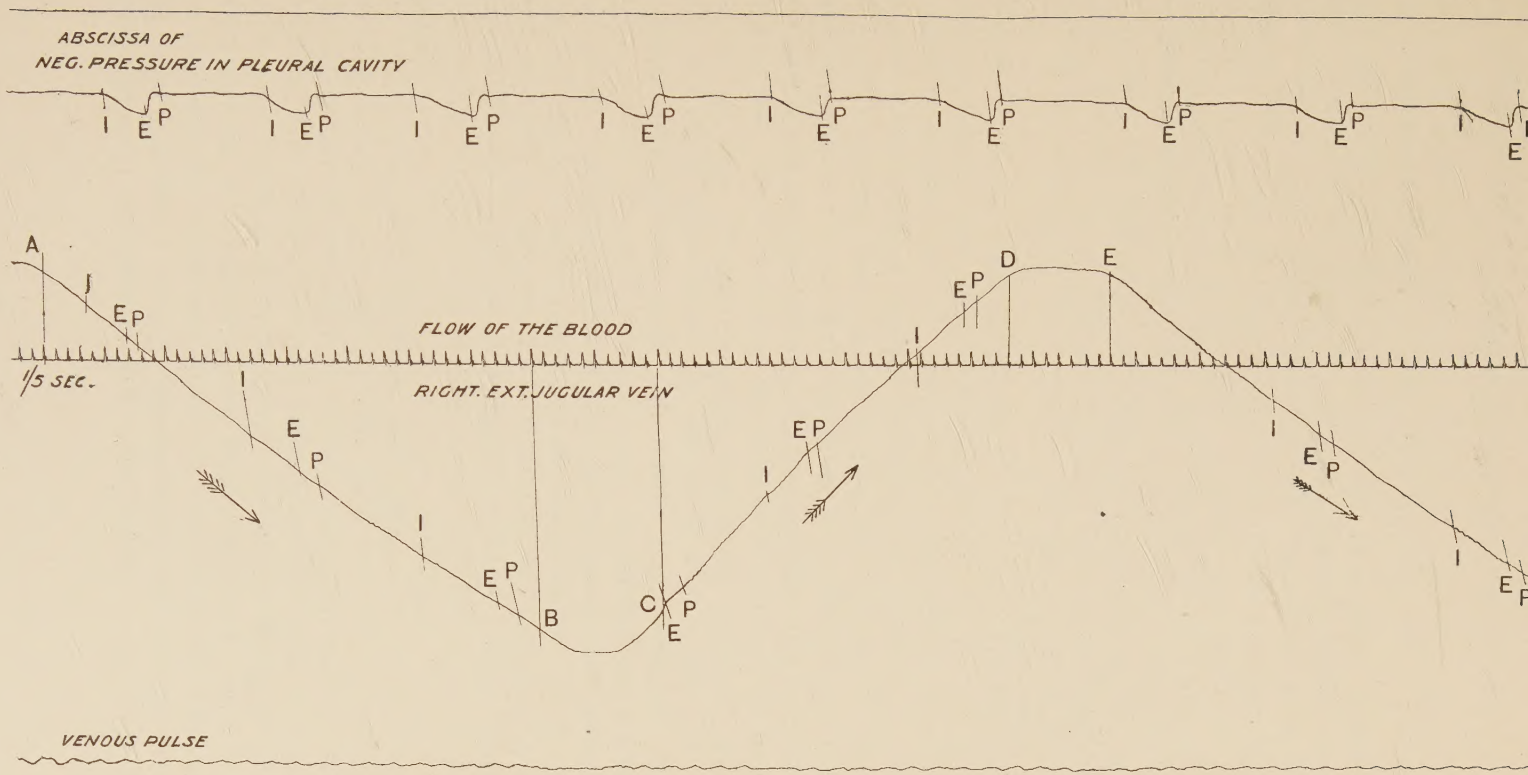

FIGURE 2. — The blood-flow in the external jugular vein.

The Volume and the Velocity of the Blood-Stream.

In making quantitative determinations of the blood-flow, especially in a vein, it is of course essential to reduce the resistance of the piston to a minimum. The external jugular vein being in an easily accessible position, the stromuhr could be placed horizontally. Thus, the blood was forced to make only a short lateral curve to enter the cylinder instead of being driven to a considerable height above the vein. The resistance was further decreased by counterpoising the writing-lever, indirectly therefore also the piston. A weight, just failing to move the piston by its own gravity, was placed upon the lever when moving downward and removed when the upward phase commenced.

In four of the experiments of this group the stromuhr, containing a warm 0.7 per cent sodium cloride solution, was inserted opposite the fifth to seventh rings of the trachea. In the fifth experiment its position was higher, the peripheral cannula being inserted close to the point of union of the internal and external maxillary veins. To prevent the possible entrance of air all parts of the stromuhr were made secure with beeswax and the opening for the piston was surrounded by a capsule filled with soft vaseline. It was also thought advisable to ligate the large communicating vein upon the larynx. The experiments were performed on medium-sized dogs, the right jugular vein being used exclusively. They were anæsthetized with morphine and chloroform.

In calculating the volume all variations in the blood-flow, dependent, as we shall see later, upon the respiratory changes in the intrathoracic pressure and the contraction of the right side of the heart, have been neglected. Only the relation of the height of the entire phase to its duration has been taken into account. Moreover, to avoid errors due to coagulation, only those phases were measured that were written during two minutes; the blood in the cylinder was still fluid from four to five minutes after the beginning of the experiment.

The internal diameter of the vein, necessary in calculating the velocity, was obtained by the method employed by Tschuewsky in the investigation referred to previously. A short portion of the vessel having been exposed, its outside diameter was determined by means of a spring caliper. The entire vessel was subsequently compressed between two narrow glass plates, the compression being just sufficient to let no blood pass. The thickness of the glass plates

was then subtracted from this measurement and the newly-derived value subtracted from the outside diameter.

The results of the experiments are given in Table I. The quantities obtained by measuring the various phases are reduced to a uniform value in each case, namely, the number of cubic centimetres per second.

TABLE I.

THE VOLUME AND THE VELOCITY OF THE BLOOD-STREAM.

Exp.	Weight of dog in kilos.	Volume. c.c. per sec.	Inside diameter. Mm.	Velocity. Mm. per sec.
1	10	1.8	0.4	143
2	12	2.1	0.42	146
3	12	2.4	0.43	163
4	13	1.9	0.4	151
5	21	3.7	0.6	131
Average	13	2.4	0.45	147

THE EFFECT OF STIMULATION AND SECTION OF THE VAGUS.

By stimulating either vagus with a sufficiently strong current the blood-flow can be made to cease, as can readily be seen by a glance at Fig. 3. In this experiment the left nerve was stimulated for about five seconds, the distance of the coils being 10 cm. (medium stimulus) The current was made at *A* and broken at *B*. A comparison with the abscissa will show that the blood-flow ceases a short time after the passage of the current and resumes its former value immediately after *B*.

The reverse relationship may be obtained by using a strong current of longer duration. In this case the blood-flow will stop almost the instant the current is made, but will not immediately become normal again. The curve after breaking the current will then show a staircase arrangement, indicating thereby that the strongly stimulated heart regains its normal frequency only gradually.

A staircase curve will also be written when the current applied to the vagus is weak, *i. e.*, not sufficiently strong to stop the heart entirely, but only to separate its beats more widely.

Such a curve is shown in Fig. 4. The current (distance of coils 15 cm., duration about three seconds) was made at *A* and broken at *B*. Three heart-beats, weaker than normal and of longer duration, occurred during this period. A less than normal onward flow is

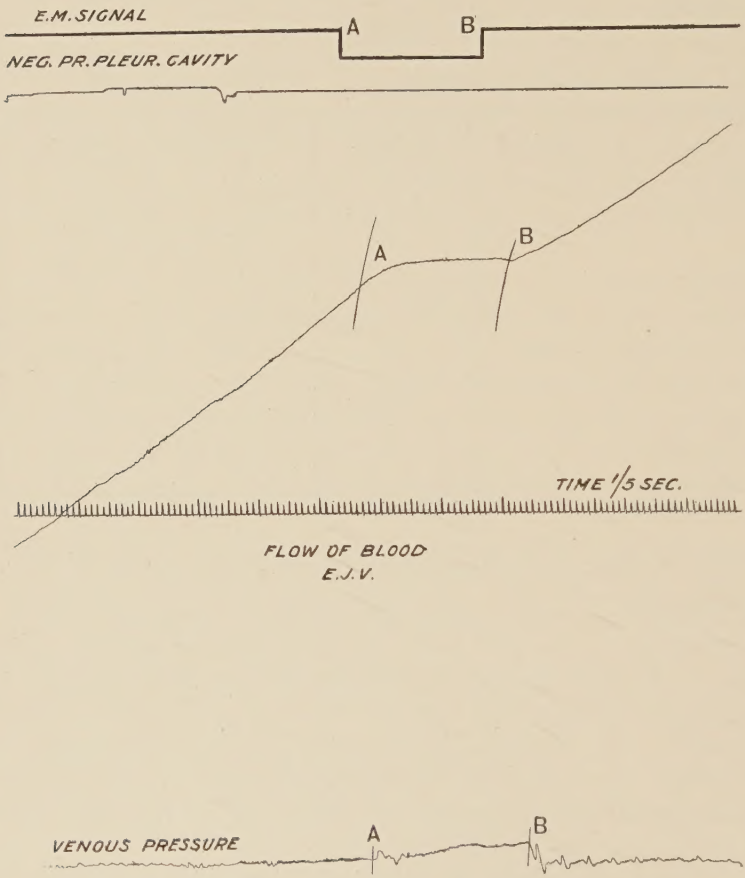

FIGURE 3. — Stimulation of left vagus (from *A* to *B*) with medium current.

observed to have taken place during the active period of the heart, from 1 to 2, while scarcely any flow was present during the pause, from 2 to 1. After discontinuing the stimulation the blood-flow regained its normal value again.

In two of the experiments both vagi were suddenly divided with scissors, while the curve of the blood-flow was being written. The

individual phases immediately became much steeper, showing thereby that a greater volume of blood was passing through the vein. A comparison was then made between the normal volume of blood and that propelled after the section of this nerve. The results of this calculation are contained in Table II.

TABLE II.

THE VOLUME OF BLOOD BEFORE AND AFTER SECTION OF THE VAGI.

Exp.	Weight of dog in kilos.	*A.* Normal flow. c.c. per sec.	*B.* Flow after section of vagi. c.c. per sec.	Increase. *B* times *A*.
1	10	1.8	5.9	3.2
2	8	1.2	2.8	2.4

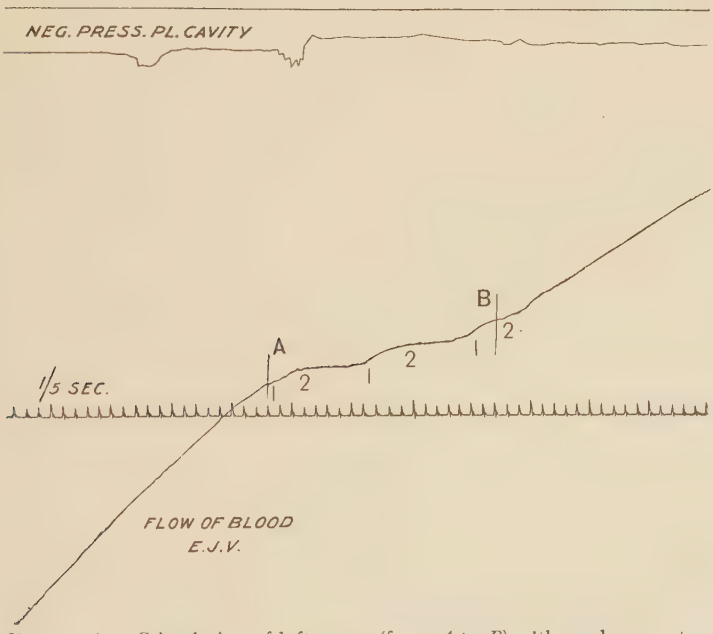

FIGURE 4. — Stimulation of left vagus (from *A* to *B*) with weak current.

THE CHANGE IN THE BLOOD-FLOW DURING THE COMPRESSION OF BOTH CAROTID ARTERIES.

Both carotid arteries were previously placed in ligatures opposite the third tracheal ring and were suddenly compressed during the ex-

periment by being tightly drawn against the flat ends of two probes. The great decrease in the blood-flow of the external jugular vein, produced by the compression, is clearly betrayed in Fig 5. The ligatures were tightened at *A* and released at *B*.

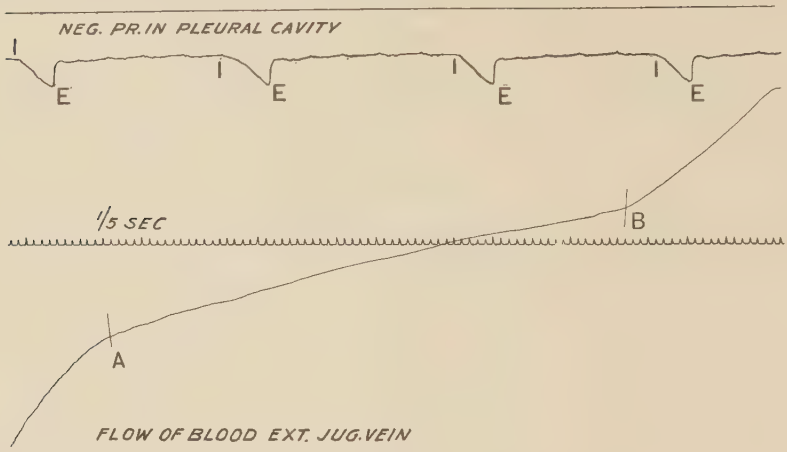

FIGURE 5. — Compression of both carotid arteries (from *A* to *B*).

This procedure was repeated several times in three different animals. In Table III. the normal volume of blood is compared with that passing through this vein during the compression.

TABLE III.

THE EFFECT OF COMPRESSION OF BOTH CAROTID ARTERIES.

Exp.	Weight of dog in kilos.	Normal volume. c.c. per sec.	Volume during compression. c.c. per sec.	Per cent of decrease.
1	8	1.5	0.7	53
2	10	1.7	0.68	60
3	10	1.8	0.87	52
Average	9	1.66	0.75	57

Among the conclusions arrived at so far, the following may be emphasized:

1. The normal volume of the blood-stream in the external jugular vein in a dog, weighing 13 kilos, is about 2.4 c.c. per second and the velocity 147 mm. per second.

2. By stimulating the vagus a total cessation of flow may be produced.

3. Section of both vagi increases the volume of the blood-stream 2.8 times.

4. By compressing both carotid arteries the quantity of blood in the external jugular vein is reduced 57 per cent.

The Respiratory Variations in the Blood-flow.

The curve of the blood-flow, as recorded by the lever of the stromuhr, is not a straight line, but shows regular periodic variations. The quantity of blood propelled is therefore not equally large at all times.

Two distinct types of variations will be considered in this paper, namely, those due to the changes in intrathoracic pressure during respiration, and secondly, those produced by the activity of the right auricle and ventricle. A third class, including all those changes in the venous flow that are dependent upon accidental causes, such as muscular contractions either near or more or less remote from the vein experimented on, will be reserved for future consideration.

In order to eliminate as much as possible the influence of the heart, the stromuhr in these experiments was inserted in the upper portion of the jugular, immediately below the union of the internal and external maxillary veins. Thus, a greater number of valves were interposed between the central cannula and the central venous trunks. This type of variations was most distinctly marked in those animals having a feeble heart-action normally or in those in which the anæsthetic had a depressing effect upon this organ.

The changes in intrathoracic pressure were recorded by a tambour, connected by means of a cannula with the left pleural cavity. The downward phase of the respiratory curve corresponds therefore to inspiration and the upward phase to expiration.

Fig. 6 is an example of this type of variations. We observe that the curve of the blood-flow shows regular and periodic deviations from its otherwise straight diagonal course, first turning further away from the abscissa and then further toward it. The changes occur at *I*, *E*, and *P*. We have therefore a period of increased flow, lasting from *I* to *E* and a period of slackened flow, extending between *E* and *P*. At the latter point the blood-flow assumes its normal value again.

When the ordinates of the negative pressure curve are compared with those of the blood-flow, it becomes evident that the variations

occur synchronously with the respiratory movements. During inspiration the flow is greater than normal and during expiration the flow is less than normal. Moreover, the increase takes place immediately

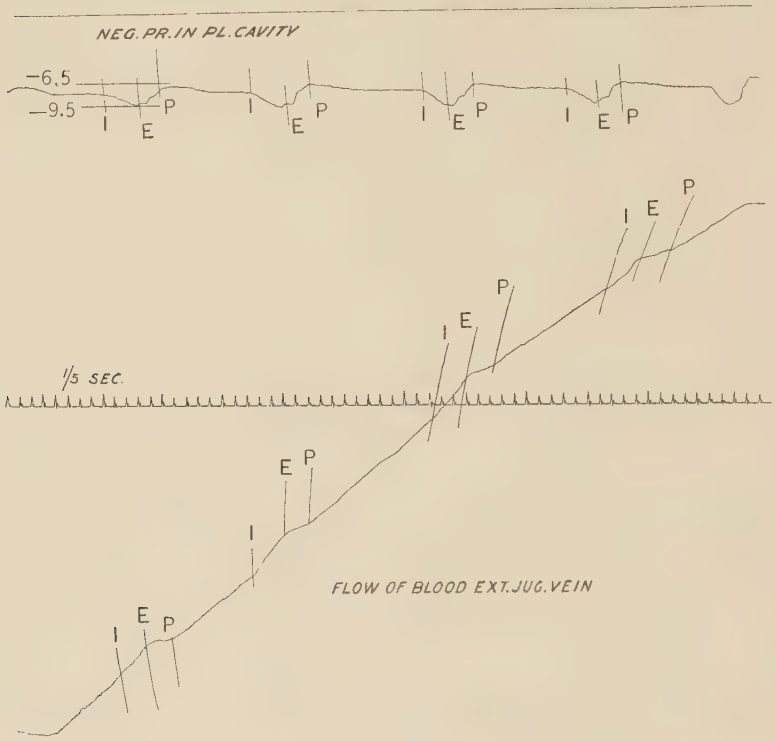

FIGURE 6. — The respiratory variations.

on inspiration, but becomes greater in the course of this phase, reaching its maximum value at the time of greatest negative pressure. The same parallelism is displayed during the expiratory phase. The shorter this phase, the shorter the duration of the period of decreased flow and the more decided the changes in the intrathoracic pressure, the more conspicuous are the changes in the blood-flow. Thus, forced expiration can produce a stoppage in the flow.

To show the dependence of the respiratory variations on the depth of the respiratory movements, the values for the following three experiments have been calculated. Table IV. shows the duration of the respiratory phases as recorded by the tambour connected with the pleural cavity.

TABLE IV.

THE RELATION OF THE DEPTH OF THE RESPIRATORY MOVEMENTS TO THE VARIATIONS IN THE BLOOD-FLOW.

Exp.	Normal flow (during pause). c.c. per sec.	Inspiration.			Expiration.		
		Time (sec.).	Neg. pressure. Mm. Hg	Blood-flow. c.c. per sec.	Time (sec.).	Mg. pressure. Mm. Hg	Blood-flow. c.c. per sec.
1	1.7	0.95	−6.5 to − 9.5	2.6	0.4	− 9.7 to −6.5	1.2
2	1.2	1.0	−2.5 to −10.0	2.3	0.2	−10.0 to −2.5	0.0
3	2.4	1.5	−8.0 to −10.2	2.5	0.5	−10.2 to −8.0	2.1

The respiratory pause begins at *P*. The volume of the blood-stream during this period depends of course entirely upon the activity of the heart. Consequently we must come to the conclusion that under normal conditions the heart forms by far the most important factor in propelling the blood, while the respiratory movements play

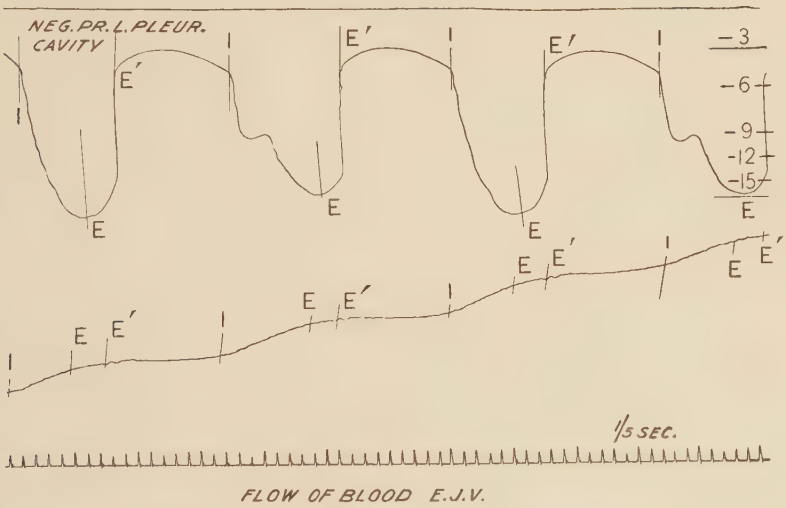

FIGURE 7. — The effect of forced respiratory movements.

only a secondary part. But, as their influence upon the blood-stream increases with their depth, it must necessarily also follow that they become the more important, the shorter the respiratory pause. How important they may become at times is clearly shown in Fig. 7.

This curve was written immediately after section of the left vagus in a lightly anæsthetized animal.

Normally the negative pressure in the pleural cavity varied from −4 to −8.25 mm. Hg and the curve of the blood-flow resembled very closely that given in Fig. 6. Immediately after the section the negative pressure showed the usual wider range toward as well as away from the abscissa (from −3 to −15 mm. Hg), but, instead of the usual decrease in the frequency of respiration, the section in this instance produced — at least for a short time — much quicker movements. The forced character of expiration is shown by the fact that the upper convex portion of the curve gradually approaches very near to the abscissa ; a true pause is therefore absent.

The important influence of this type of respiration on the blood-flow in the jugular is apparent at the first glance. The curve has completely lost its normal character, represented in Fig. 6. To be sure the inspiratory movement is accompanied by a decided onward flow of the blood (*I* to *E*) which becomes most conspicuous during the time of greatest negative pressure. The period of slackened flow during expiration is not stopped at *E*, however, but continues as the negative pressure decreases still further. Finally, when the negative pressure reaches its lowest value, almost a complete stop in the blood-flow occurs. During the period of gradually increasing negative pressure, prior to the decided inspiratory movement at *I*, a correspondingly greater volume of blood is again moved onward. During the forced expiratory phase beginning at *E*, therefore, the part which the heart plays in propelling the blood was masked.

The Effect of Stimulation of the Phrenic Nerves.

Having found that the respiratory variations in the blood-flow are so closely related to the changes in the intrathoracic pressure, stimulation of the nervi phrenici was resorted to for the purpose of producing even more decisive changes in pressure. Both nerves were placed in covered electrodes opposite the outer border of the lower fourth of the sterno-cleido-mastoid muscle. A brief tetanic current was used, the strength of which was altered in such a way that either a slight or a great increase in intrathoracic pressure resulted. The current was made synchronous with the beginning of inspiration.

Fig. 8 may serve as an example of weak stimulation of these nerves. The current was in this case applied three times in succession (*A* to *B*)

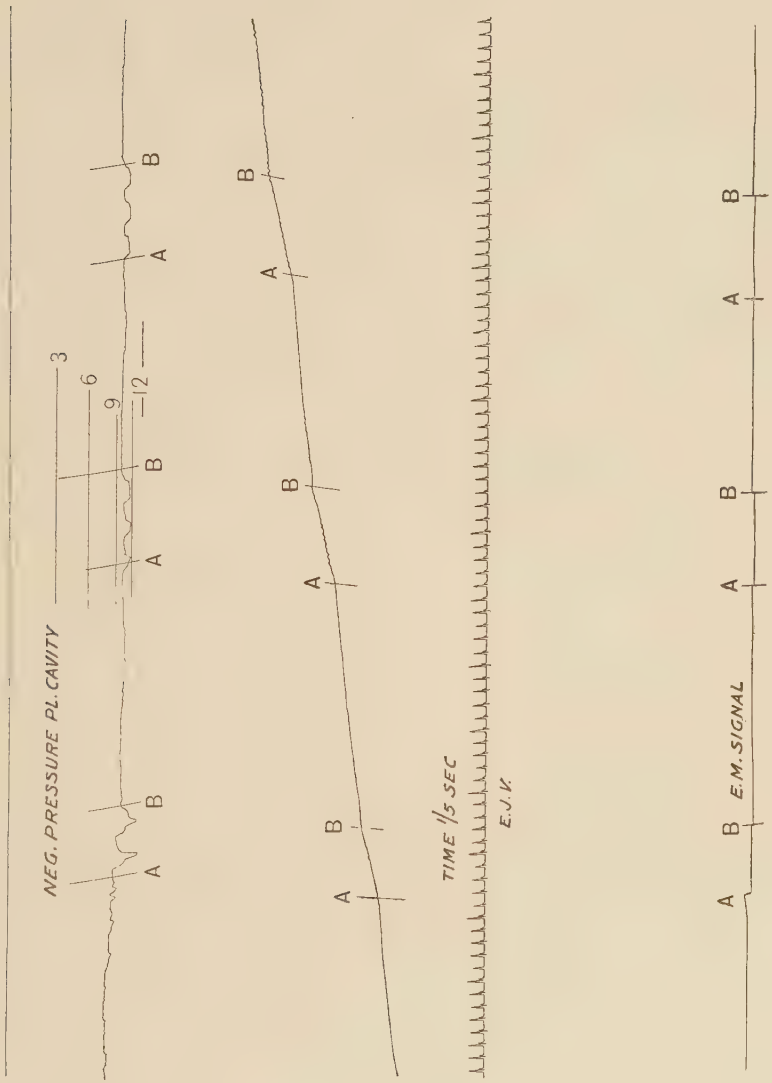

FIGURE 8. — Weak stimulation of the phrenic nerves.

and was sufficiently strong to increase the negative pressure to —12 mm. Hg, while normally it varied from —4.25 to —8 mm. Hg. The change in the blood-flow produced thereby was very decided. While normally only 1.2 c.c. per second were propelled, the average value during the periods of increased negative pressure (*A* to *B*) amounted to 1.9 c.c. per second.

In another case the intrapleural pressure was increased from —9.25 mm. Hg to —13 mm. Hg by stimulating the phrenic nerves. The blood-flow suffered at the same time an increase from 1.8 c.c. to 2.4 c.c. per second.

Increasing the negative pressure still further by stimulating these nerves with a strong current does not necessarily imply that a correspondingly larger quantity of blood is thereby moved onward. In fact, under these conditions the blood-flow usually decreases somewhat. In Fig. 9, for instance, the volume of blood was reduced from

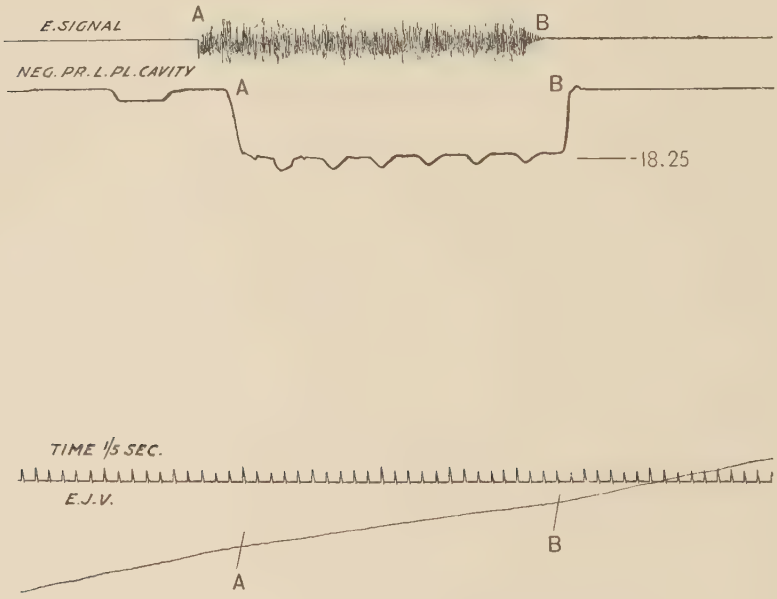

FIGURE 9. — Strong stimulation of the phrenic nerves.

1.8 c. c. to 1.6 c.c. per second during the period of stimulation from *A* to *B*. The negative pressure at this time was increased from its normal value, —9.25, to —18.25 mm. Hg. It seems that in these instances the strongly contracted diaphragm presses upon the

abdominal organs, increasing in this way the flow in the inferior vena cava and lessening the influx of blood from the external jugular.

The Cardiac Variations in the Blood-flow.

The variations to be considered in this chapter are wholly dependent upon the changes in intra-auricular pressure occurring during each cardiac cycle. It is only natural to assume that the pressure-curve in the central venous trunks pursues a parallel course to that of the auricle, and that in the tributary veins these changes must be the more conspicuous, the closer we approach this venous reservoir.

Undoubtedly, under normal conditions the suction-action of the right auricle and ventricle on the blood in the great veins is the most important factor in the onward movement of the blood within them. The inspiratory movement by reason of its lesser frequency can be considered only as an "occasional" aid. The cardiac variations in the blood-flow of this vein will be recorded best when the respiratory movements are shallow and far apart and the heart beats forcibly.

In these experiments the stromuhr was inserted in the lower portion of the vein. Its central cannula, placed well into the groove between the neck and the shoulder, remained outside of the thoracic cavity and about 4 to 5 cm. from the subclavian vein. Three or four valves were thus left intact between the stromuhr and the inferior extremity of this vein. No valves were found between the latter point and the auricle.

The respiratory phases were recorded as described above. The venous pulse was recorded by a membrane manometer, connected by means of a T tube with the central cannula of the stromuhr. This record served me in obtaining the various phases of the cardiac cycle.

Venous pulsation may be due first to the contraction of the right auricle and ventricle, secondly to various accidental mechanical influences, and thirdly — at least in the smaller veins — to the arterial pulse. It is apparent that in these experiments only the first type has to be considered.

In interpreting the venous pulse curve obtained in these experiments I made use of the investigation of Fredericq[1] which, so far as

[1] Fredericq, L.: Travaux du Laboratoire de Liège, 1889–90, x, pp. 85–107.

I know, is the only recent paper on this subject. Fredericq recognizes two distinct rises in the venous pulse; the first he attributes to the systole of the right auricle and the second to the ventricular contraction. In general, the curves obtained by me correspond very closely with those in the paper referred to. Only one difference should be spoken of, and that is the fact that the auricular contraction always gave a strong rise, much higher than that of ventricular systole. In this respect the curve is identical with the curve of intra-auricular pressure shown in Fig. 10.

But it seemed essential that the curve of the blood-flow be compared directly with the curve of intra-auricular pressure. This, it seems to me, can be done without hesitation. In the paper cited above, Fredericq comes to the conclusion that the pressure-curve of the external jugular exhibits essentially the same characteristics as that of the right auricle.

Before proceeding further it might be well to consider briefly the different characteristic points of the intra-auricular pressure curve. According to Porter,[1] whose results substantiate and extend those of Fredericq, the auricular curve consists of:

A. The systolic rise, corresponding to the contraction of the auricle.

B. The first diastolic fall, corresponding to the relaxation of the auricle.

C. The first diastolic rise, from near the beginning of ventricular systole to the opening of the semilunar valves.

D. The second diastolic fall, from the opening of the semilunar valves to near the beginning of ventricular relaxation.

E. The second diastolic rise, from the end of the second diastolic fall to the beginning of ventricular relaxation.

F. The third diastolic fall, during some portion of ventricular relaxation.

G. The pause, from the third diastolic fall to the next systolic rise.

Upon this curve I shall largely rely in harmonizing the different features of the variations of the blood-flow with the changes in intra-auricular pressure.

Fig. 11 is an example of the type of variations to be dealt with in this chapter. The entire line recording the blood-flow exhibits numerous depressions similar in form and recurring at regular intervals. Between these indentations the curve pursues a wavy

[1] Porter, W. T.: Journal of physiology, 1892, xiii, pp. 513–555.

course upward, first ascending very rapidly and then extremely slowly. We observe, therefore, that the flow is not equally great at

FIGURE 10. — Curve of intra-auricular pressure, taken with a large cannula in the auricular appendix (PORTER).

A. Systolic rise.
A.–B. First diastolic fall.
B.–C. First diastolic rise.
C.–D. Second diastolic fall.
E. Second diastolic rise.
F. Third diastolic fall.
G. Pause.

1. Beginning of auricular systole.
2. Beginning of ventricular systole.
3. Opening of semilunar valves.
5. Beginning of ventricular downstroke.
6. End of ventricular downstroke.

all times. There is a period during which a great quantity of blood is moved onward and a period during which very little flow takes place. Records taken at a greater speed (Fig. 12), in which the details of the curve are rendered visible, will show that in this second period there are times when the flow is completely arrested. These will be discussed below.

A comparison between the ordinates of the respiratory phases and those of the blood-flow in Fig. 11 will show immediately that the variations seen here are absolutely different from those described in the preceding chapter. But, if the ordinates of the blood-flow are compared with those of the venous pulse a complete correspondence is seen to exist.

The first elevation in the venous pulse curve, numbered 1, 2, etc. corresponds exactly with the bottom of the notch in the curve of the blood-flow, 1, 2, etc. The end of the period of slight flow is therefore synchronous with the end of auricular systole. As soon as the diastolic phase of this cavity begins, the blood-flow is greatly increased, from 1, 2, etc., to 1′, 2′, etc. The latter ordinates indicate the end of the period of greatest negative pressure during auricular diastole. Thus we see that the period of increased flow (1, 2, etc., to 1′, 2′, etc.) coincides with the entire diastolic phase of the auricle, from the end of auricular systole to the beginning of the second diastolic rise. From 1′, 2′, etc., to 1, 2, etc., a very slight rise in the curve of the blood-flow is noticeable. This period of slight flow commences with the second diastolic rise and ends with the next auricular systole.

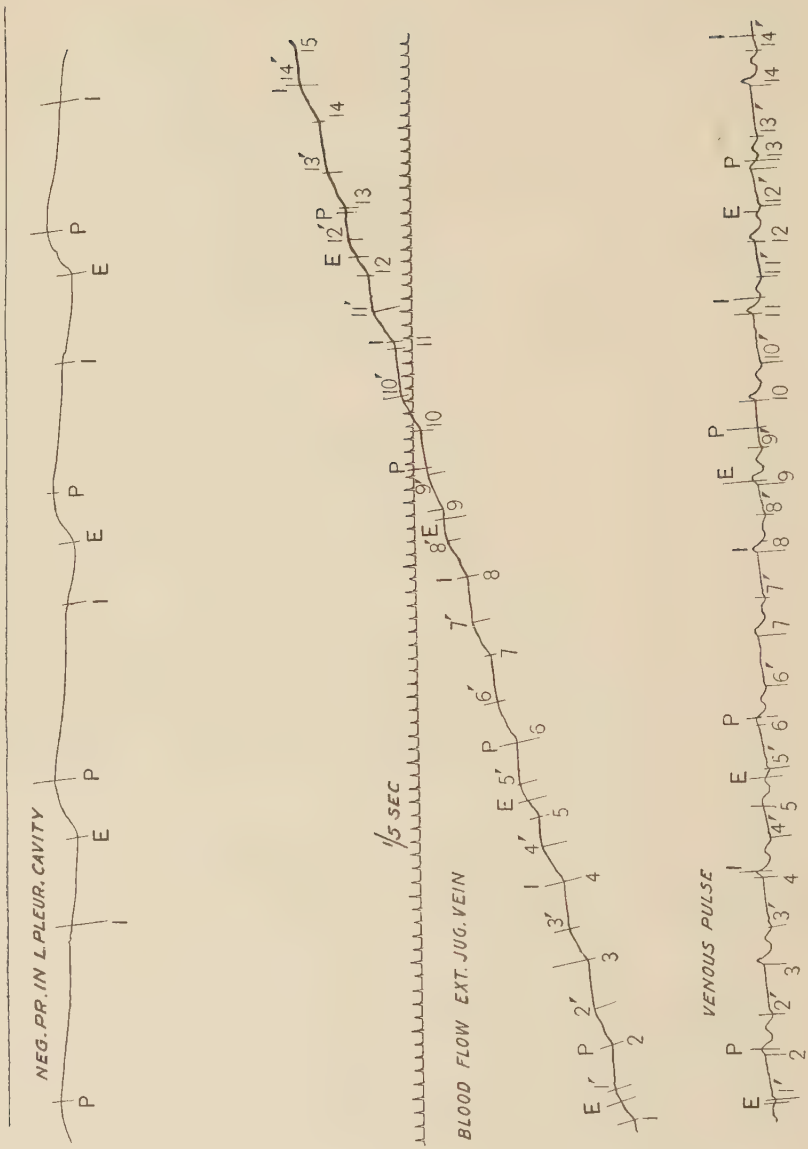

FIGURE 11. — The cardiac variations in the blood-flow.

A more careful inspection of the curve will also reveal the presence of a second slight notch about midway between the end of auricular systole (1, 2, etc.), and the end of the second diastolic fall (1′, 2′, etc.). This depression, shown clearly in only a few of the intersystolic phases of this curve, coincides with the beginning of ventricular systole. But, to show the full significance of this indentation and also to bring out more clearly the several features of the curve, it is necessary to study a curve written upon a rapidly revolving drum (Fig. 12).

FIGURE 12. — The cardiac variations.

When the different phases of the auricular cycle are in this way forced more widely apart, each intersystolic period shows the following details: The fall in pressure following the auricular systole is accompanied by an increase in the blood-flow (*A–B*) which continues during the entire first diastolic fall (*A–B*). During the first diastolic rise, *i.e.*, from the beginning of ventricular contraction to the opening of the semilunar valve, no onward movement of blood occurs, (*B–C*). The second diastolic fall (*C–D*), following the opening of these valves, produces a renewed increase in the blood-flow, which is again stopped during the second diastolic rise (*D–E*). There is another noticeable rise in the curve of the blood-flow at *E*, but it is much slighter than the two preceding and very likely takes place during *F–G*, the third diastolic fall. The quantity of blood propelled during the common pause (*F–G*) is extremely small. During the auricular systole (*G–A*) no onward movement of blood occurs.

François-Frank[1] inserted a Chauveau's hæmodromograph in the external jugular vein and found that the systole of the auricle does not cause the column of blood to move backward. When he, however, destroyed the valves centrally to the instrument a backward movement of the blood took place. He therefore concluded that normally such an occurrence is made impossible by the interposition of the venous valves. He further states that a cessation of flow does not take place during this period.

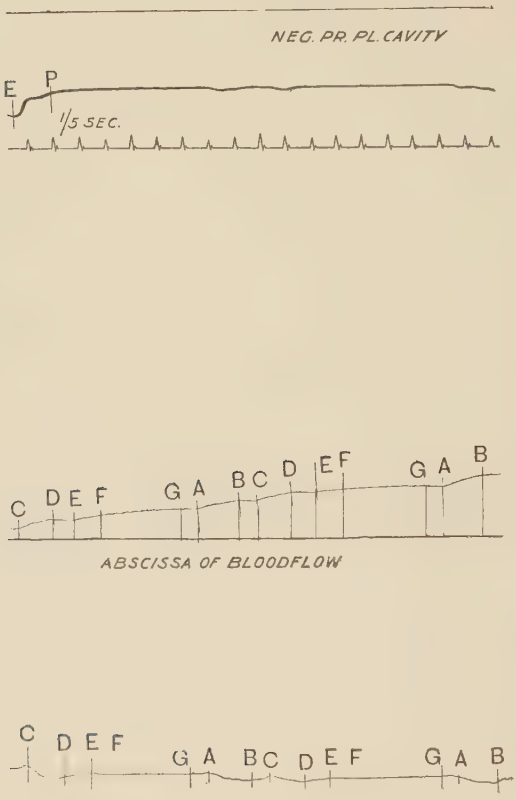

FIGURE 13. — The cardiac variations.

While the experiments now under consideration prove the former statement to be correct, no evidence is contained in the curves to show that a stoppage in the blood-flow does not occur. When the abscissa is drawn and the ordinates of the curve of the blood-flow are continued downward, it can readily be seen that this curve pursues a parallel course to the abscissa in three places, namely, from *G–A*, from *B–C*, and from *D–E*. (Compare Fig. 13.)

When these periods are compared with the curve of auricular pressure it is found that no onward movement of blood in the external jugular vein takes place:

1. During the systole of the auricle,
2. During the first diastolic rise,
3. During the second diastolic rise.

[1] FRANÇOIS-FRANK, C. A.: Archives de physiologie, 1890, pp. 347–354 and pp. 395–410.

Thus, we must conclude that the volume of blood in this vein enters the central venous trunks and right auricle only during the periods of lesser pressure, namely:

1. During the first diastolic fall,
2. During the second diastolic fall,
3. During the third diastolic fall,
4. During the pause common to both auricle and ventricle.

These conclusions confirm and extend the results gained in Porter's study of the effect of changes in auricular and ventricular pressure upon the filling of the heart: He concluded from the origin of the systolic and the first diastolic rise, that the auricular pressure at these moments is higher than the pressure in the contiguous veins and that the venous inflow must at these times cease (page 525). With regard to the second diastolic rise his observations did not enable him to speak with confidence.

Regarding the third diastolic fall and the pause common to both auricle and ventricle, we have previously seen that the blood-flow during the third diastolic fall (E to F) is much less than during the first two periods of falling pressure. During the pause hardly any flow is noticeable.[1]

The main factor in propelling the blood must therefore be the first and second diastolic falls. The second diastolic fall appears to exercise an even greater suction-action than the first. Although no exact determinations were made, this statement is well substantiated by the largest number of the curves. It harmonizes with the fact that according to Porter a greater fall in pressure occurs during this period. (Compare Fig. 10 and also page 533 of Porter's paper referred to previously.)

To show the relative importance of the various periods of the curve of auricular pressure I have calculated the value of the blood-flow (c.c. per second) for the first and the second half of each auricular cycle. The first half embraces the first diastolic fall, first diastolic rise, and second diastolic fall. The second half includes the values from the beginning of the second diastolic rise to the end of the next systolic rise. In the curves of Figs. 12 and 13 these periods are marked from A to D and from D to A. In the curve of Fig. 11 the first period extends from 1, 2, etc., to 1′, 2′, etc., and the latter period

[1] In two experiments there was hardly any increase in the blood-flow, even during the third diastolic fall. The force of the heart undoubtedly produces some slight alterations at times.

from 1′, 2′, etc., to 1, 2, etc. From thirty to forty intersystolic phases taken upon a rapid-moving drum, were measured in each case. This number seemed sufficient, because the individual deviations are very slight.

TABLE V.

THE RELATIVE VALUES OF THE BLOOD-FLOW FOR THE FIRST AND SECOND HALVES OF AN AURICULAR CYCLE.

Exp.	Weight of dogs in kilos.	Duration of first period from *A* to *D* (sec.).	Volume of blood. c.c. per sec.	Duration of second period from *D* to *A*.	Volume of blood. c.c. per sec.	Duration of auricular cycle in sec.	Volume of blood. c.c. per sec.
1	9	0.37	1.75	0.32	0.15	0.69	1.9
2	12	0.5	2.15	0.6	0.25	1.1	2.4
3	9	0.49	1.7	0.51	0.10	1.0	1.8

This table serves to prove again the observation made previously that by far the greatest volume of blood is moved onward during the first half of the auricular cycle, *i. e.*, during the period of greatest fall in pressure. During the second half, including the third diastolic fall and the common pause, the blood-flow is minimal. We observe that the former volume is about ten times as great as the latter.

This fact is of the highest importance to the frequent heart. For, when the heart beats quickly, the common pause is reduced in duration or entirely absent. It can readily be seen that only a very slight loss to the volume of inflowing blood is occasioned by the absence of the pause. Indeed, the auricular cycle might be reduced to about one-half its normal duration and still there would not be an important decrease in the volume of the inflowing blood, so long as the duration of the first two diastolic falls remained unchanged.

Porter's measurements, on pages 531 to 533 of the paper already cited, show that the duration of the second diastolic fall remains practically unchanged even in the most frequent heart and that only the succeeding part of diastole, including the pause, suffers the shortening in time.

And even if the second diastolic fall should be slightly shortened when the heart beats very quickly and without a corresponding decrease in the length of the systolic periods, the loss in blood which

would in this case occur might be compensated by a correspondingly greater fall in pressure.

In order to show more clearly the relationship between the changes in intra-auricular pressure and the cardiac variations in the blood-flow, I have placed my curve, showing the volume of the blood-flow

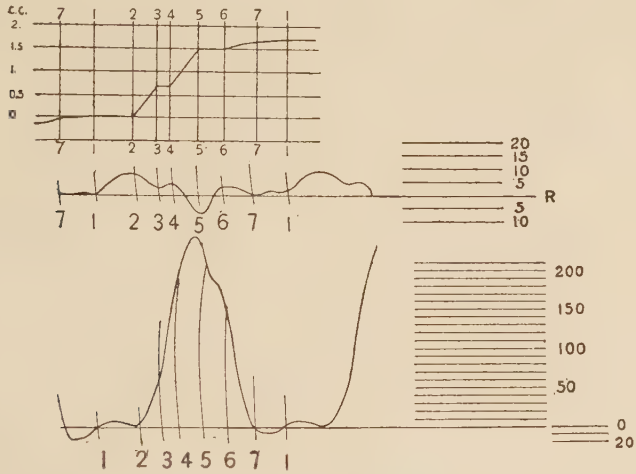

FIGURE 14. — The blood-flow in the external jugular vein in relation with the auricular and ventricular pressure curves. The uppermost curve shows the volume of blood flowing through the external jugular vein from the measurements in the present investigation. The middle and lowermost curves are respectively the intra-auricular and the intra-ventricular pressure curves, simultaneously recorded. The calibration of the auricular and ventricular membrane manometers are shown at the side. (PORTER, W. T., Figs. 1, 2, and 13, Plate XVIII.)

1–2. Systolic rise.	First cessation of flow.
2–3. First diastolic fall.	First period of great flow.
3–4. First diastolic rise.	Second cessation of flow.
4–5. Second diastolic fall.	Second period of great flow.
5–6. Second diastolic rise.	Third cessation of flow.
6–7. Third diastolic fall.	Period of slight flow.
7–1. Common pause.	Slight flow, or stoppage.

through the external jugular vein, above the curves of pressure in the auricle and ventricle. (Fig. 14.) The time of the auricular cycle is one second and the quantity of blood propelled during this entire period is 1.7 c.c. The relative volumes for the different phases are given in 0.1 c.c.

Before concluding the discussion of the variations in the blood-flow, reference must be made to the changes which are produced by the simultaneous appearance of the respiratory and cardiac variations.

In Fig. 15 we observe that by far the largest number of the cardiac variations occur during the respiratory pause. Only two (3 and 7) coincide with respiratory phases. After the second and seventh systolic rises (auricular systoles) the blood-flow shows the usual increase (2 to *I* and 7 to *I*), but the succeeding period of slight flow during the last half of the auricular cycle is not present. Instead, there is an even greater onward flow (*I* to *E*), which entirely destroys the depression that would otherwise occur during this secondary rise.

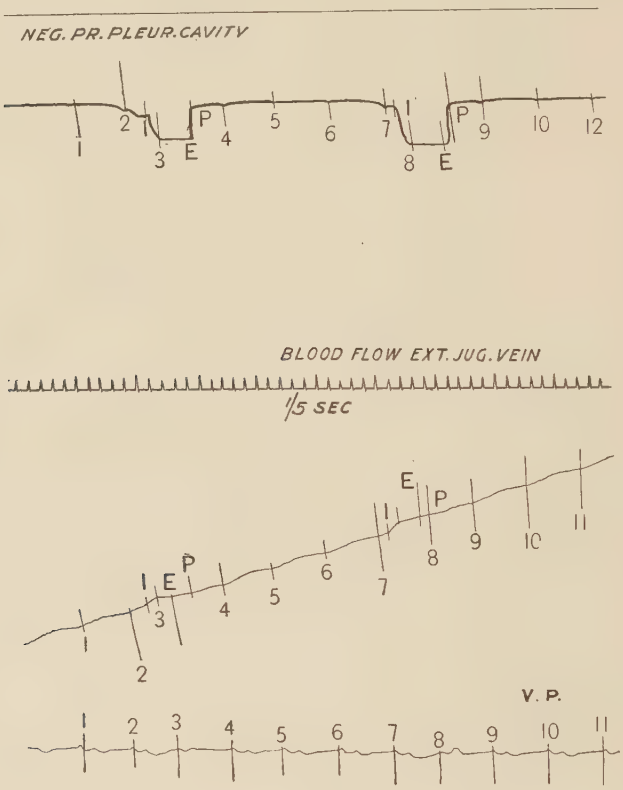

FIGURE 15. — The cardiac and respiratroy variations.

The greater fall in intravenous pressure occasioned by the inspiratory movement (*I* to *E*) interferes therefore with the normal formation of the cardiac variations and gives rise to a blood-flow which is proportional to the sum of the intravenous pressures, caused by the force of the heart and by the depth of inspiration.

The same summation by interference occurs during the expiratory movement, but so soon as the respiratory pause commences, the cardiac variations again become prominent.

Summary.

1. The normal volume of the blood-stream in the external jugular vein in a dog weighing 13 kilos amounts to about 2.4 c.c. per second. The velocity is 147 mm. per second.

2. By stimulating the vagus a total cessation of flow can be produced.

3. Section of both vagi increases the volume of the blood-stream 2.8 times.

4. By compressing both carotid arteries the quantity of blood is reduced 57 per cent.

5. The blood-flow in the external jugular vein is intermittent.

6. Two types of variations are present, namely those due to the respiratory movements and those caused by the changes in pressure during each auricular cycle.

7. Inspiration quickens the flow, expiration lessens it. The conspicuousness of the respiratory variations is dependent upon the frequency and the depth of the respiratory movements.

8. By increasing the intrapleural negative pressure slightly by stimulating the phrenic nerves the blood-flow is exaggerated. Strong stimulation of these nerves, on the other hand, generally produces a retardation.

9. During each auricular cycle the blood-flow ceases when the periods of rising pressure occur. The flow during the first and second diastolic falls is about ten times as great as during the other phases; therefore, in the frequent heart the duration of the entire cycle may be reduced to more than one-half before an appreciable loss in the quantity of inflowing blood would result. The second diastolic fall is more important than the first.

10. When the respiratory and cardiac pressure changes occur synchronously, the volume of the blood-stream is determined by the combined influence of both factors.

Reprinted from the American Journal of Physiology.
Vol. IX. — May 1, 1903. — No. III.

MUSCULAR CONTRACTION AND THE VENOUS BLOOD-FLOW.

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TWO distinct groups of variations in the venous blood-flow are recognizable. The first group embraces those variations in the blood-volume which occur periodically, either with the changes in intra-auricular pressure during each cardiac cycle, or with the changes in intra-thoracic pressure during each respiratory phase.[1] The second group embodies all those variations which are dependent upon accidental, mechanical causes and do not appear at regular intervals. The latter may therefore be termed "irregular" variations.

Leaving out of consideration those obvious changes in the venous flow which result from external mechanical influences, the present paper deals with only the most important class of variations of the latter type; namely, with those produced by the contraction of skeletal muscles.

Briefly outlined, the method consisted in determining quantitatively the volume of the blood-flow, first under normal conditions and subsequently during the different stages of muscular contraction. The femoral vein was used in these experiments, because this vessel is easily isolated and drains a complex of muscles, the nerves of which are readily accessible to the electrodes. The blood-volume was measured by means of Hürthle's recording stromuhr.[2]

The experiments were performed on medium-sized dogs in morphine-ether narcosis. The nerves of the posterior extremity to be experimented on were previously placed in covered electrodes. The sciatic nerve was exposed where it leaves the pelvis, the obturator nerve as it passes across the median surface of the adductor femoralis magnus muscle, and the "crural" nerve at some point of its course along the femoral vessels (saphenous nerve).

[1] Burton-Opitz, R: This journal, 1902, vii, pp. 435–459.

[2] Hürthle, C.: Compte rendu du cinquième congrès international de physiologie, Turin, 1901; A short description of this instrument is also given in the paper cited previously.

The animal was placed upon its back with the posterior extremities slightly flexed and abducted. The toes of the leg experimented on were loosely fastened to a flexible rod.

The femoral vein was isolated from the groin down to the entrance of the vena femoralis posterior superior. In this preparation a very small vein, draining the fatty tissue below the groin, was destroyed. When present, another small vein entering the main vessel nearly opposite the latter was ligated, but those veins found in the immediate neighborhood of the groin were compressed only during the insertion of the stromuhr. The stromuhr, filled with a warm normal saline solution, was placed vertically. Its central cannula came to lie close to the small veins near the groin, while its peripheral cannula remained at some distance from the orifice of the vena femoralis posterior superior.

In those experiments in which the effect of compression of the femoral artery on the blood-flow in the corresponding vein was tried, the artery was placed in a ligature opposite the central cannula of the stromuhr; *i. e.*, about three centimetres below the groin. The artery was raised and compressed between the forceps.

Compression of the femoral vein, peripherally to the orifice of the vena femoralis posterior superior, was also employod. The latter vein drains the largest mass of the gracilis muscle, and thus, by stimulating the obturator nerve, the effect of the contraction of a single muscle on the venous blood-flow could be determined.

Upon the smoked paper of the kymograph were recorded the curve of the blood-flow and the time-curve, written by a Jaquet chronometer in fifths of seconds. The latter record served at the same time as the abscissa of the former. The duration of the stimulation of nerves was marked by an electro-magnetic signal. The respiratory movements were recorded by a tambour communicating with the left pleural cavity. In most of the experiments the venous pressure was also recorded. For this purpose Hürthle's venous manometer was connected by means of a T tube with the peripheral cannula of the stromuhr. The pressure was therefore recorded between the muscles and the instrument.

The Normal Flow in the Femoral Vein.

It seems advisable to consider first the normal volume of the blood-flow and subsequently the changes which result in consequence of

muscular contraction. The average value being obtained, a more ready comparison can be made between the normal blood-flow and the flow during a muscular contraction.

The lever of the recording stromuhr of Hürthle writes a continuous curve, composed of upward and downward phases. The writing lever passes in the former direction, if the piston in the central cylinder is driven downward by the blood entering through the opening in the roof of the stromuhr. But if by turning the disc below the floor of the instrument, the blood is forced into the lower part of the cylinder, the piston travels upward and the writing lever records in this case a curve from above downward.

In Tables I to IX the value of the blood-stream is calculated for about one half the total number of phases of each experiment. The duration of each phase and the total quantity of blood propelled during this time having been obtained, these values were reduced to cubic centimetres per second. The latter figures were then employed in calculating the average value of the blood-stream for each experiment.

In order to avoid all errors due to coagulation only about twenty phases were included in the calculation, a number sufficient to obtain a good average. Those variations in the curve, dependent upon the cardiac and respiratory activity,[1] were wholly disregarded; only the duration and height of the entire phase were measured.

As those phases during which compression of the femoral artery was resorted to, would have necessitated a different arrangement of the tables, they are inserted separately after the experiments to which they belong. Those phases, during which stimulation of the nerves of the posterior extremity was tried, are indicated in the tables, but will be considered separately in a later chapter. The last four experiments of this series show the effect of nerve-section on the blood-flow in this particular vein. A sufficient number of normal phases having been recorded, the nerves enumerated above were quickly divided with the scissors, and another series of phases written.

The other details, it seems to me, can easily be derived from Tables I to IX.

[1] Even at such a great distance from the heart the cardiac variations in the blood-flow were often very conspicuous, but naturally their amplitude is less here than in the external jugular vein. The same may be said regarding the respiratory variations.

TABLE I. EXPERIMENT I.

Weight of dog, 16½ kilos. Left femoral vein used.

No. of phase.	Duration of phase in seconds.	Total vol. of blood during phase. c.c.	Volume. c.c. per second.	Remarks.
1	5.1	8.1	1.59	
2	5.0	7.2	1.44	
3	8.6	8.7	1.01	
4	7.9	8.3	1.05	
5	7.2	7.2	1.00	
6	8.0	8.0	1.00	
7	7.0	8.5	1.21	
8	..	..	..	Compression of femoral artery.
9	8.3	6.9	0.83	
10	..	..	..	Compression of femoral artery.
11	7.9	9.0	1.14	
12	8.0	8.0	1.00	
13	8.2	8.1	0.98	
14	5.4	5.4	1.00	
15	..	..	..	Compression of femoral artery.
16	9.1	8.3	0.91	
17–19	..	..	..	Stimulation of sciatic nerve, tetanic current.
20	..	..	..	Compression of femoral artery.
21	7.2	8.0	1.11	
22	7.8	8.3	1.06	
23	8.2	7.8	0.95	

Highest value, 1.59; lowest value, 0.83; average value, 1.08 c.c. per sec.

EXPERIMENT I. Compression of the femoral artery.

No. of phase.	Duration of compression in seconds.	Total quantity of blood during compression. c.c.	Volume. c.c. per second.	Average value. c.c. per second.	Av. value of normal blood-flow. c.c. per second.	Decreases during compression. Per cent.
8	5.2	0.47	0.09	0.10	1.08	90
10	12.1	1.28	0.10			
15	11.6	1.18	0.10			
20	6.7	0.89	0.13			

TABLE II. EXPERIMENT II.

Weight of dog, 13 kilos. Left femoral vein used.

No. of phase.	Duration of phase in seconds.	Total vol. of blood during phase. c.c.	Volume. c.c. per second.	Remarks.
1	7.2	6.0	0.83	
2	14.5	10.8	0.75	
3	13.1	11.5	0.87	
4	..	..	..	Compression of femoral artery.
5	12.8	10.1	0.79	
6	14.9	10.8	0 72	
7	13.6	9.0	0.66	
8	..	..	..	Compression of femoral artery.
9	12.5	9.0	0.72	
10a	..	..	..	Compression of femoral vein.
10b	..	..	..	Stimulation of obturator nerve, tetanic current.
11a	..	..	..	Compression of femoral vein.
11b	..	..	..	Stimulation of obturator nerve, tetanic current.
12	12.3	10.6	0.86	
13	14.5	11.3	0.77	
14	13.6	12.1	0.88	
15	13.9	12.0	0.86	
16	15.9	11.0	0.69	
17–20	..	..	..	Stimulation of sciatic nerve, tetanic current.
21	13.6	9.7	0.71	
22	12.3	9.5	0.77	

Highest value, 0.88; lowest value, 0.66; average value, 0.77 c.c. per sec.

EXPERIMENT II. Compression of femoral artery.

No. of phase.	Duration of compression in seconds.	Total vol. of blood during compression. c.c.	Volume. c.c. per second.	Average value. c.c. per second.	Av. value of normal blood-flow. c.c. per second.	Decrease during compression. Per cent.
4	8.1	1.3	0.16	0.18	0.77	76
8	10.7	2.2	0.20			

TABLE III. EXPERIMENT III.

Weight of dog, 14 kilos. Right femoral vein used.

No. of phase.	Duration of phase in seconds.	Total vol. of blood during phase. c.c.	Volume. c.c. per second.	Remarks.
1	19.6	11.8	0.60	
2	20.5	11.6	0.56	
3	..	..	..	Compression of femoral artery.
4	17.5	11.1	0.63	
5	17.0	12.1	0.71	
6	16.0	9.2	0.57	
7a	..	..	..	Compression of femoral vein.
7b	..	..	..	Stimulation of obturator nerve, single induction.
8	15.0	8.7	0.58	
9	14.3	10.5	0.73	
10	18.7	9.2	0.49	
11	..	..	..	Stimulation of sciatic nerve, single induction.
12	16.1	11.0	0.68	
13	16.9	11.9	0.70	
14	..	..	..	Stimulation of sciatic nerve, single induction.
15	14.0	10.9	0.77	
16	15.3	9.7	0.63	
17a	..	..	..	Compression of femoral vein.
17b	..	..	..	Stimulation of obturator nerve, tetanic current.
18	18.2	10.6	0.58	
19	17.2	10.0	0.57	
20	..	..	..	Compression of femoral artery.
21	..	..	..	Stimulation of sciatic nerve, tetanic current.
22	..	..	..	Compression of femoral artery.

Highest value, 0.77; lowest value, 0.49; average value, 0.63 c.c. per sec.

EXPERIMENT III. Compression of femoral artery.

No. of phase.	Duration of compression in seconds.	Total vol. of blood during compression. c.c.	Volume. c.c. per second.	Average value. c.c. per second.	Av. value of normal blood-flow. c.c. per sec.	Decrease dur. compression. Per cent.
3	5.2	1.3	0.25	0.23	0.63	63
20	5.4	1.4	0.26			
22	5.3	1.1	0.20			

TABLE IV. EXPERIMENT IV.

Weight of dog, 12½ kilos. Left femoral vein used.

No. of phase.	Duration of phase in seconds.	Total vol. of blood during phase. c.c.	Volume. c.c. per second.	Remarks.
1	14.0	9.1	0.65	
2	11.8	9.6	0.81	
3	..	..	..	Compression of femoral artery.
4	11.5	9.6	0.83	
5	11.6	8.2	0.70	
6a	..	..	..	Compression of femoral vein.
6b	..	..	..	Stimulation of obturator nerve, single induction.
7	13.5	9.1	0.67	
8	12.4	8.6	0.69	
9	10.5	9.2	0.87	
10	..	..	..	Stimulation of sciatic nerve, single induction.
11	11.5	8.4	0.73	
12	..	...	..	Stimulation of sciatic nerve, single induction.
13	13.2	8.5	0.64	
14	11.7	8.2	0.70	
15	13.0	9.0	0.69	
16	..	..	..	Stimulation of sciatic nerve, tetanic current.
17	15.0	11.0	0.73	
18	..	..	..	Stimulation of sciatic nerve, tetanic current.
19	12.8	11.0	0.86	
20	14.4	10.1	0.70	
21	12.9	9.7	0.75	
22a	..	..	..	Compression of femoral vein.
22b	..	..	..	Stimulation of obturator nerve, tetanic current.
23	7.0	5.4	0.77	

Highest value, 0.87; lowest value, 0.64; average value, 0.73 c.c. per sec.

EXPERIMENT IV. Compression of femoral artery.

No. of phase.	Duration of compression in seconds.	Total vol. of blood during compression. c.c.	Volume. c.c. per second.	Average value. c.c. per sec.	Av. value of normal blood-flow. c.c. per sec.	Decrease dur. compression. Per cent.
3	14.7	3.2	0.21	0.21	0.73	71

TABLE V. EXPERIMENT V.

Weight of dog, 17 kilos. Right femoral vein used.

No. of phase.	Duration of phase in seconds.	Total volume of blood during phase. c.c.	Volume. c.c. per sec.	Remarks.
1	6.5	7.7	1.18	
2	6.4	8.3	1.29	
3	7.5	8.2	1.09	
4	7.9	9.5	1.20	
5	8.1	9.0	1.11	
6	..	..	..	Stimulation of sciatic nerve, single induction.
7	6.9	8.7	1.26	
8	5.8	8.0	1.38	
9	6.2	8.0	1.29	
10	6.9	9.0	1.30	
11	7.8	9.1	1.16	
12	6.7	8.0	1.19	
13	8.1	8.7	1.07	
14	8.8	9.1	1.03	
15	..	..	..	Stimulation of sciatic nerve, single induction.
16	6.2	7.6	1.22	
17	..	..	..	Stimulation of sciatic nerve, single induction.
18	7.0	7.9	1.12	
19	7.2	8.5	1.18	
20	8.0	8.6	1.07	
21	8.0	9.0	1.12	

Highest value, 1.38; lowest value, 1.03; average value, 1.18 c.c. per sec.

TABLE VI. EXPERIMENT VI.

Weight of dog, 14½ kilos. Left femoral vein used.

No. of phase.	Duration of phase in seconds.	Total volume of blood during phase. c.c.	Volume. c.c. per sec.	Remarks.
1	7.1	5.6	0.79	
2	10.1	8.5	0.84	
3	5.5	6.9	1.25	
4	9.7	12.1	1.24	
5	10.1	10.2	1.00	
6	8.1	9.1	1.12	
7	9.5	10.4	1.09	
8	8.2	7.7	0.93	
9	10.5	11.4	1.08	
10–13	..	..	..	Stimulation of sciatic nerve, tetanic current.
14	9.8	12.7	1.29	
15	9.1	10.0	1.09	
Normal flow: highest value, 1.29; lowest value, 0.79; *average value*, 1.06 c.c. per sec.				
16–17	..	..	..	*Sciatic, obturator, and crural nerves cut.*
18	3.2	11.8	3.6	
19	4.2	12.1	2.8	
20	4.1	10.2	2.4	
21	3.2	12.2	3.8	
22	3.4	9.5	2.8	
23	3.0	12.0	4.0	
24	3.6	11.6	3.2	
25	4.1	11.4	2.7	
26	3.8	11.6	3.0	
Flow after nerve-section: highest value, 4.0; lowest value, 2.4; *average value*, 3.1 c.c. per sec.				

TABLE VII. EXPERIMENT VII.

Weight of dog, 12 kilos. Left femoral vein used.

No. of phase.	Duration of phase in seconds.	Total volume of blood during phase. c.c.	Volume. c.c. per sec.	Remarks.
1	19.3	10.0	0.52	
2	25.0	12.2	0.49	
3	..	..	..	Stimulation of sciatic and obturator nerves, tetanic.
4	19.3	11.2	0.58	
5	18.0	12.4	0.68	
6	20.5	11.6	0.56	
7	22.2	10.3	0.46	
8	..	..	..	Stimulation of obturator nerve, tetanic.
9	21.7	12.0	0.55	
10	20.1	12.5	0.62	
11	..	..	..	Stimulation of sciatic and obturator nerves, tetanic.
12	20.9	10.8	0.51	
Normal flow: highest value, 0.68; lowest value, 0.46; *average value*, 0.55 c.c. per sec.				
13–14	..	..	..	*Sciatic and obturator nerves cut.*
15	8.3	12.6	1.51	
16	7.3	10.2	1.39	
17	7.9	10.7	1.35	
18	6.4	11.3	1.76	
19	8.0	10.1	1.26	
20	5.3	7.7	1.45	
21	7.5	11.7	1.55	
22	6.4	9.0	1.40	
23	6.4	9.1	1.42	
24	4.5	7.8	1.51	
Flow after nerve-section: highest value, 1.76; lowest value, 1.26; *average value*, 1.46 c.c. per sec.				

TABLE VIII. EXPERIMENT VIII.

Weight of dog, 18 kilos. Left femoral vein used.

No. of phase.	Duration of phase in seconds.	Total volume of blood during phase. c.c.	Volume. c.c. per sec.	Remarks.
1	8.7	10.6	1.21	
2	9.2	10.2	1.10	
3	9.5	11.5	1.21	
4	7.1	11.1	1.56	
5	9.5	12.0	1.26	
6	10.2	10.5	1.02	
7	8.1	9.0	1.11	
8	9.3	10.8	1.16	
9–13	..	..	..	Stimulation of nerves, single induction.
14	9.4	9.5	1.01	
15	8.3	11.4	1.37	
Normal flow: highest value, 1.56; lowest value, 1.01; *average value*, 1.20 c.c. per sec.				
16–18	..	..	..	*Sciatic, obturator, and crural nerves cut.*
19	3.7	11.9	3.21	
20	2.7	10.1	3.73	
21	3.4	10.2	3.00	
22	2.8	8.2	2.92	
23	3.8	11.7	3.07	
24	3.2	10.0	3.12	
25	3.5	12.1	3.45	
26	3.0	10.5	3.50	
27	3.2	9.8	3.06	
28	3.6	10.6	2.94	
Flow after nerve-section: highest value, 3.73; lowest value, 2.92; *average value*, 3.20 c.c. per sec.				

TABLE IX. EXPERIMENT IX.

Weight of dog, 11 kilos. Right femoral vein used.

No. of phase.	Duration of phase in seconds.	Total volume of blood during phase. c.c.	Volume. c.c. per sec.	Remarks.
1	18.6	9.5	0.51	
2	21.7	10.0	0.46	
3	20.4	10.2	0.50	
4	19.1	11.5	0.60	
5	..	..	..	Stim. of sciatic and obturator nerves, tetanic current.
6	22.0	10.8	0.49	
7	25.4	12.0	0.47	
Normal flow: highest value, 0.60; lowest value, 0.46; *average value*, 0.50 c.c. per sec.				
8–9	..	..	..	*Sciatic and obturator nerves cut.*
10	6.4	8.7	1.35	
11	5.9	10.3	1.74	
12	6.2	10.7	1.72	
13	5.9	9.5	1.61	
14	6.3	10.5	1.66	
15	7.2	11.1	1.54	
16	7.3	10.8	1.47	
Flow after nerve section: highest value, 1.74; lowest value, 1.35; *average value*, 1.58 c.c. per sec.				

The most important facts derived from Tables I to IX are more comprehensively arranged in Table X. This outline, however, also includes the velocity of the blood-stream for five of the experiments, this value being given in millimetres per second.

In obtaining the internal diameter of the vein, necessary in this calculation, I have again employed the method which Tschuewsky [1]

[1] Tschuewsky, F. A.: О Кровоснабженіи Отдѣльныхъ Органовъ (On the blood-supply of several organs), Charkow, 1902.

made use of in his investigation on the blood-flow in different arteries. Although far from being exact, it was the most suitable for these experiments. The outside diameter of the vein having been determined by means of calipers, the vein was lightly compressed between two narrow plates of glass. The thickness of the glass-plates being deducted from this measurement gives the thickness of the vessel wall, which in turn is deducted from the outside diameter of the vein.

TABLE X.

THE FLOW OF THE BLOOD IN THE FEMORAL VEIN.

Experiment.	Weight of dog. Kilos.	A. Normal volume of blood. c.c. per sec.	B. Volume during compression of femoral artery. c.c. per sec.	Per cent of decrease during compression.	C. Volume after section of nerves. c.c. per sec.	Increase C. times A.	Internal diameter of vein in mm.	D. Velocity of blood stream. mm. per sec.
1	16.5	1.08	0.10	90	..	..	4.3	74.7
2	13	0.77	0.18	76	..	..	4.0	61.3
3	14	0.63	0.23	63	..	..	..	..
4	12.5	0.73	0.21	71	..	..	..	..
5	17	1.18	..	..	..	..	5.0	60.1
6	14.5	1.06	..	..	3.10	2.9	..	..
7	12	0.55	..	..	1.46	2.6	3.8	48.5
8	18	1.20	..	..	3.20	2.6	4.9	63.7
9	11	0.50	..	..	1.58	3.1	..	..
Av. values.	14.2	0.85	0.18	75	2.33	2.8	4.4	61.6

Among the conclusions derived from the preceding table the following may be emphasized. We observe first that in spite of the large calibre of the vein, the blood-volume is rather small. It varies from 0.50 c.c. per second in a dog, weighing 11 kilos, to 1.20 c.c. per second in a dog, weighing 18 kilos. The average value of the blood-flow, as obtained in the above nine experiments, is 0.85 c.c. per second; the average weight, 14.2 kilos.

Although the correspondence between the weight of the animal and the blood-volume is not brought out very strikingly in these ex-

periments, the table at least strongly suggests that in general the volume of the blood-flow increases and decreases in proportion to the weight of the animal.

If a comparison is made between the volume of the blood-stream in the femoral and that in the external jugular vein, it is found that the former is considerably smaller. The eight experiments[1] which I made to determine the normal quantity of blood in the right external jugular vein, gave the average value of 2.03 c.c. per second. The femoral vein, therefore, carries less than one half this amount of blood.

It cannot be assumed that this difference in the blood-volume of the veins under consideration is due to corresponding differences in body-weight, because the average weight of the animals used in determining the blood-flow in the external jugular vein was 12 kilos, while that of the dogs used in the present experiments is 14.2 kilos. Although smaller than the external jugular, the lumen of the femoral vein is of considerable size, at least its large internal diameter is not proportionate to the small quantity of blood traversing this vessel.

In the pamphlet referred to previously Tschuewsky gives a series of experiments on the blood-flow in the femoral artery. The average value of the blood-volume in seven dogs, ranging in weight from 12.5 to 14.5 kilos, is 0.63 c.c. per second. Two other dogs, weighing 37.0 and 51.0 kilos respectively, showed a flow of 1.2 c.c. and 1.0 c.c. per second. If the average value for the venous flow (0.85 c.c. per second) is compared with that of the arterial (0.65 c.c. per second), it is found to be slightly greater. The difference, amounting to only 0.2 c.c. per second, could easily be explained by referring to the differences in the weight of the dogs; those used in the present experiments being the heavier. However, it is also noticed that in the vein the maximal value of 1.0–1.2 c.c. per second was obtained already in dogs weighing only 16 to 18 kilos. These facts suggest that even normally the volume of blood traversing the vein is slightly greater than that of the corresponding artery. It is, however, not absolutely correct to draw these conclusions from two different sets of experiments, or animals.

In support of the previous statement the following fact might be cited: If the femoral artery is compressed opposite the stromuhr, the blood-flow in the vein does not cease completely. The quantity of

[1] Burton-Opitz: This journal, 1902, vii, Experiments 1 to 5, on page 439; Experiment 2, on page 441; and Experiments 1 and 2, on page 442.

blood still propelled must therefore reach this vein in an indirect way by means of anastomosing vessels. It is possible that even normally a slight quantity of blood reaches the vein in this manner.

The reduction in the volume of the blood-stream, produced by the procedure just mentioned, is not uniform. In the experiments given above the decrease varied from 63 to 90 per cent. In another experiment not inserted above, because the record was accidentally destroyed, the decrease amounted to only 51 per cent. Thus, the compression caused in this case a reduction in the blood-flow of only about one half its former volume.

From what has been said regarding the normal blood-flow and the diameter of the femoral vein, it can readily be concluded that the velocity of the current is very slight. The five experiments inserted above have given an average value of 61.6 mm. per second. If the velocity of the venous current is compared with that in the corresponding artery (134.4 mm. per second)[1] it is found to be about one half as great.

After section of the nerves innervating the posterior extremity, the phases written by the lever of the stromuhr immediately became much steeper, indicating thereby that a greater quantity of blood traversed the vein. In the Experiments VI to IX in which this procedure was tried the resulting flow was from 2.6 to 3.1 times greater than the normal (average 2.8 times greater).

A comparison between the quantitative determinations of the venous and arterial blood-flow shows that the insertion of the stromuhr into a vein is not such a serious procedure as might be supposed at first. At least, if any impediment to the venous circulation is produced thereby, it is not greater than that which results if this instrument is placed in an artery.

The Changes in the Normal Flow produced by Muscular Contractions.

Tetanic current. — In the preceding paragraphs we have determined the volume of the blood-flow when the muscles of the posterior extremity are at rest. The present chapter contains a consideration of those changes in the blood-flow which ensue when muscular contractions occur.

[1] See Tschuewsky's paper, page 76.

The sciatic and obturator nerves were stimulated while the curve of the blood-flow was being written. The stimulation was confined to one, or included both the nerves enumerated. Both tetanic and single induced currents were used, their strength being varied so as to produce either a strong, or a medium muscular contraction. The phases during which stimulation of the nerves was resorted to are indicated in the tables inserted previously.

Whether only one or both nerves were stimulated, the general characteristics of the variation in the blood-flow remained always the same for each kind of stimulus. Changes in the intensity of the cur-

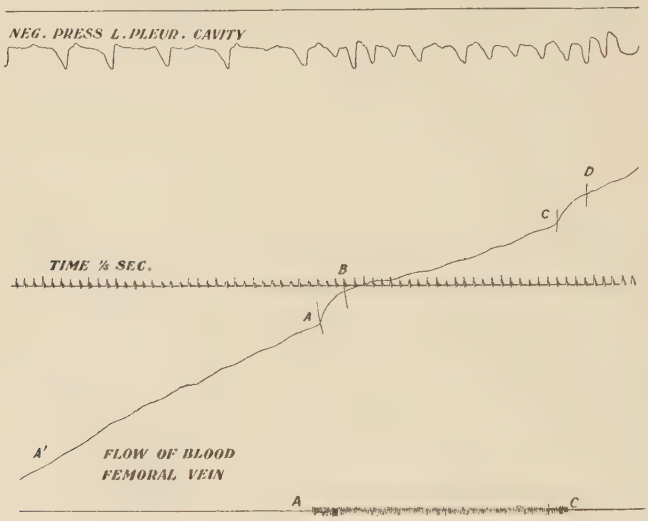

FIGURE 1.—Two-thirds the original size. Variation in the venous blood-flow during a tetanic muscular contraction.

rent also produced no alterations in the general outline of the curve. The only difference noticed under all conditions was merely one of one degree; *i. e.*, the more nerves stimulated and the stronger the current, the more evident was the variation in the blood-flow.

It seems advisable to consider first the details of a variation produced by a tetanic muscular contraction. For this purpose Fig. 1 is inserted in this place. A tetanizing current of medium strength (distance of coils, 13 cm.) was in this case applied to the sciatic nerve; duration of stimulation, about six seconds.

We observe immediately that the curve of the blood-flow (from *a'*

to *a*) becomes very steep at *a*, suggesting thereby that a great increase in the volume of the blood-stream has taken place. When the ordinates are compared, this point is found to correspond with the moment of stimulation. At *b* the opposite effect is noticeable. The decrease in the flow beginning here continues to *c*, to the moment of breaking the current. Furthermore, it is evident that the flow becomes greater than normal immediately on discontinuing the stimulation; the curve showing for a brief period a greater incline than the normal (*c* to *d*). Eventually, however, the blood-flow returns to its normal value.

The period of great onward movement, occurring after the application of the current (*a* to *b*), is therefore synchronous with the period of muscular shortening. It is noticed, moreover, that the quantity of blood forced into the vein is greater during the first part of this period than during its latter half, when the muscles have nearly reached their maximal degree of contraction. Apparently, this increase in the blood-volume is due solely to the pressure of the contracting muscular substance upon the mass of blood contained in its vessels.

As soon as the point of maximal shortening has been reached (*b*) the curve inclines strongly toward the abscissa, indicating thereby that the blood-flow is less than normal (*b* to *c*). The decrease in the flow is most conspicuous during the first part of this period, while, if the stimulation is continued for a longer time, a slight and gradual increase above the previous value is noticeable during its latter half. This slight rise becomes the more evident, the longer the muscles are kept in the contracted state. The tetanic muscle therefore is an obstacle to the blood-flow, but when in the course of a longer stimulation the muscle becomes relaxed by fatigue, a steadily increasing quantity of blood is enabled to pass.

The complete relaxation of the muscles on breaking the current is followed by a brief period of increased venous flow (*c* to *d*), after which the normal value is again slowly established. Considered quantitatively, this gush-like rise, after removing the hindrance to the blood-flow, is always much smaller than that occurring during the shortening of the muscles (*a* to *b*).

The entire variation in the venous blood-flow produced by a tetanic muscular contraction may therefore be divided into the following phases:

1. Period of great flow, synchronous with the muscular shortening (*a* to *b*).

2. Period of slight flow, continuing during the contracted state of the muscle (*b* to *c*).

3. Short period of increased flow, following the relaxation of the muscle (*c* to *d*).

The question how the venous blood-flow is altered by a tetanic muscular contraction has previously been investigated by Sadler[1] and subsequently by Gaskell.[2] The latter author enlarged upon the work of the former by bringing the changes in the blood-volume into relation with the alterations in the form of the muscle. He isolated the vein, draining the largest mass of the musculus vasti and musculus cruralis and measured by a special device the quantity of blood escaping from this vessel, before and during the contraction of the muscles mentioned. As far as the general characteristics of the changes observed by Gaskell are concerned, the results obtained by means of the stromuhr completely substantiate those found by the method just cited.

To show that the retardation of the blood-stream following the maximal muscular shortening (*b* to *c*) is not due to the compression of the larger vessels between the entire complex of muscles, but is caused by mechanical obstacles within each muscle, the following experiment was repeatedly tried. Both the arterial and venous trunks were isolated from all surrounding tissues from the groin downward to the musculus gracilis. The femoral vein was then compressed peripherally to the orifice of the vena musculus gracilis, so that the stromuhr recorded only the flow through this vessel. The musculus gracilis was tetanized by stimulation of the obturator nerve.

The variations in the blood-flow accompanying the tetanization of the gracilis muscle showed under these conditions the same outline as those obtained when the total quantity of blood was measured during the contraction of the entire posterior extremity. However, as the volume of blood was in this case much smaller, it naturally follows that the amplitude of the variations was much less.

In localizing the obstruction to the blood-flow within the muscle the observations of Heilemann[3] prove very suggestive. This author studied the circulation in the musculus submaxillaris of the frog under

[1] Sadler, W.: Arbeiten aus dem physiologischen Institute zu Leipzig, 1869, pp. 77–100.

[2] Gaskell, W. H.: Arbeiten aus dem physiologischen Institute zu Leipzig, 1877, pp. 45–88.

[3] Heilemann, H.: Archiv für Anatomie und Physiologie, 1902, pp. 45–53.

the microscope. On tetanizing, or on stimulating this muscle by single induction shocks, he found that the flow was greatly retarded in those fine anastomosing venules which pass between the muscular fibres and parallel to them. Even a complete cessation of flow was observed at times, and if a strong tetanic current was used, an oscillating motion and even a backward movement of the column of blood resulted.

Differences in the force of the muscular contraction do not alter the general character of the curve. This statement is illustrated by

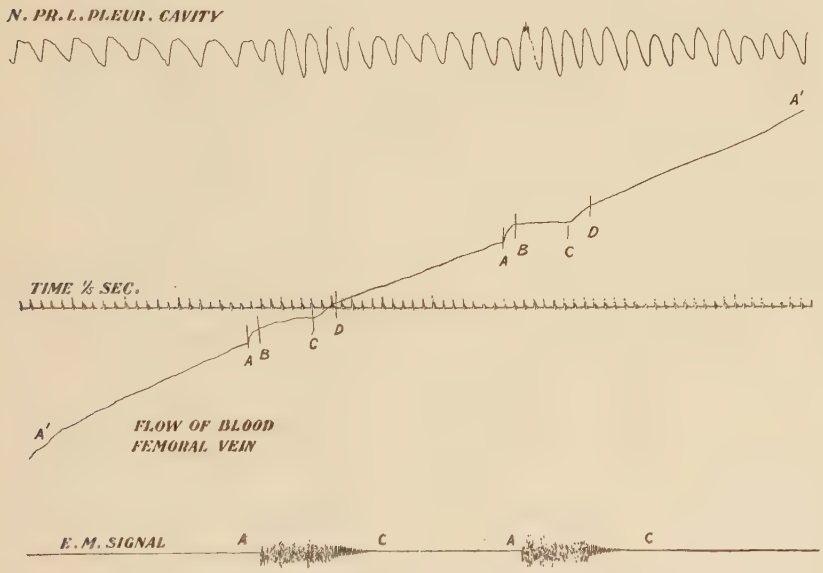

FIGURE 2. — Two-thirds the original size. Two successive variations showing different amplitude (tetanic muscular contraction).

Fig. 2. In this case two brief tetanic contractions of different strength were produced in quick succession. The sciatic nerve was stimulated first with a current of medium strength (distance of coils, 15 cm.) and subsequently with a strong current (distance of coils, 7 cm.)

We observe immediately that, although the details of the curve are the same in both cases, the changes in the blood-flow are more decisive during the strong muscular contraction. The rise of the curve on making the current (at *a*) is more sudden, steeper, and higher in the latter instance; which indicates that the volume of blood pro-

pelled during the shortening of the strongly contracted muscle is proportionately greater.

The maximal shortening having been reached (at *b*), the curve inclines more strongly toward the abscissa in the latter case; the blood-flow is therefore more effectively retarded by the strongly contracted muscle (*b* to *c*). Whether a cessation of flow can be produced by a proportionate increase in the strength of the stimulation could not be determined with accuracy, because under these conditions the muscular movements were so forcible that the stromuhr was shifted out

TABLE XI.

THE CHANGES IN THE BLOOD-FLOW DURING A TETANIC MUSCULAR CONTRACTION.

Taken from exp.	Phase.	Nerves stimulated.	Strength of current. Dist. of coils. cm.	Duration of stimulation in seconds.	Normal blood-flow. c.c. per sec.	Flow during period of musc. shortening. c.c. per sec.	Flow during tetanic state of muscle. c.c. per sec.	Flow after musc. relaxation. c.c. per sec.
1	18	sciatic	15	3.5	1.08	2.7	0.63	1.25
	19	"	7	8.1	"	4.0	0.40	1.30
2	17	"	16	7.0	0.77	1.8	0.60	0.77
	18	"	10	7.3	"	2.0	0.52	0.90
3	21	"	15	5.1	0.63	1.4	0.45	0.67
4	16	"	15	10.3	0.73	1.1	0.65	1.0
	18	"	8	5.2	"	2.5	0.39	1.0+
6	10	"	13	6.5	1.06	2.3	0.70	1.06
	12	"	7	4.1	"	3.0	0.30	1.06+
7	11	sciatic obturator	12	8.9	0.55	1.7	0.48	0.60
9	5	"	6	3.7	0.50	2.9	0.18	0.80

of its normal position. The strongest stimulus applied was: distance of coils, 6 cm.; two dry cells.

The after-effect of the tetanic contraction, consisting in the brief rise above the normal value of the blood-flow (*c* to *d*), was generally more conspicuous after the application of a strong current. In the curve now under consideration this period of increased flow is well marked in both instances, but a decided quantitative difference is not evident.

To show in a general way the pronounced differences in the blood-volume during the three principal phases of a tetanic muscular contraction, a number of these variations have been calculated, as closely as this is possible, in terms of cubic centimetres per second. The periods measured are marked in the preceding figures by the letters *a* to *b*, *b* to *c* and *c* to *d*.

Table XI also contains four instances in which the weak stimulation was followed by a stronger stimulation. The greater prominence of the changes resulting under these conditions (see Fig. 2) is clearly betrayed by these quantitative determinations.

The pressure-changes in the femoral vein, occurring during the tetanic contraction of the muscles of the posterior extremity, were recorded in most of the above experiments by means of a Hürthle's membrane-manometer (venous). This instrument, as stated before, recorded the pressure peripherally to the stromuhr.

On tetanizing the muscles the pressure quickly rose some millimetres above the normal value. At about point *b* of Figs. 1 and 2 the pressure decreased almost as rapidly as it had risen and kept subsequently very close to zero, falling generally even below the abscissa during the strong tetanic contraction. After the relaxation of the muscles the pressure remained slightly above normal for some time. If the tetanization was continued for a longer time, the pressure began to rise even before the break of the current.

The pressure-changes were also recorded in several separate experiments by means of a soda-manometer (sodium carbonate solution, specific gravity, 1.080) connected with the femoral vein by means of a T tube. A float was not used, the values being obtained by reading. The sciatic nerve was stimulated.

As is shown in Table XII, the pressure rapidly rose two to five mm. Hg above normal during the muscular shortening (*a* to *b*). The end of this period having been reached (at *b*), the pressure again decreased almost as quickly, assuming a value slightly below normal during the first part of the tetanization. Subsequently it gradually rose, remaining slightly elevated for a short time after the relaxation.

The only difference in the results of the former and latter methods consists therefore in the height of the pressure during the second period, the period of decreased flow (*b* to *c*). The soda-manometer indicated that the pressure does not drop to zero, but remains a few millimetres above the abscissa, which, it seems to me, is the correct result.

Table XII, shows, moreover, that a stronger tetanization causes a greater rise in pressure during the period of great flow, muscular shortening (*a* to *b*). We have seen previously that under these conditions the blood-volume during the second period (*b* to *c*) is even more highly reduced; however, a correspondingly greater fall in pressure during this period could not be ascertained definitely, because the differences were so very slight.

TABLE XII.

THE CHANGES IN PRESSURE IN THE FEMORAL VEIN DURING A TETANIC MUSCULAR CONTRACTION.

(The corresponding values in mm. Hg are placed in brackets.)

Experiment.	Wt. of dog. Kilos.	Duration of contr. in sec.	Strength of stimulus. Dist. of coils. cm.	Normal pressure. Mm. sod. carbonate. (Mm. Hg.)	Pressure at end of period of muscular shortening. Mm. sod. carbonate. (Mm. Hg.)	Pressure during contr. state of muscle. Mm. sod. carbonate. (Mm. Hg.)	Pressure at relaxation of muscle. Mm. sod. carbonate. (Mm. Hg.)
1	13.0	7	15	78[6.2]	100[7.9]	70[5.5]	78+[6.2+]
2	11.5	5	10	98[7.7]	140[11.1]	88[7.0]	110[8.7]
3	14.0	11	10	65[5.1]	112[8.9]	55[4.3]	78[6.2]
4	16.5	8	8	72[5.7]	132[10.5]	60[4.7]	80[6.3]
5	16.5	7	5	72[5.7]	145[11.5]	60[4.7]	80[6.3]
6	16.0	10	12	62[4.9]	85[6.7]	58[4.6]	62-[4.9-]

Single induced current. — If single induction shocks are used, the variations in the blood-flow accompanying the muscular twitches, show a somewhat different outline.

Fig. 3 may serve to illustrate the general character of the variations obtained under these conditions. The sciatic nerve was stimulated in this instance with a current of medium strength, distance of coils, 10 cm.

Both the make (*a*) and the break (*c*) of the current are followed by a considerable increase in the blood-volume which continues during the entire periods of rising energy of the muscles (*a* to *b* and *c* to *d*). Furthermore, this rise is directly proportionate to the strength of the stimulus, and therefore also to the force of the muscular contraction. The stronger the twitch, the more conspicuous is the increase in the venous blood-flow.

During the second period, *i. e.*, while the current is passing, the blood-volume is not reduced as during the tetanization of the muscles, but remains normal. The blood-flow resumes its normal value immediately after the rise occurring during the make-contraction (*a* to *b*), and retains it until the break-twitch causes another period of increased flow (*c* to *d*). Subsequent to the latter rise the blood-flow immediately returns to normal.

The fact that the blood-volume is not reduced while the current passes, greatly influences the total quantity of blood propelled in a

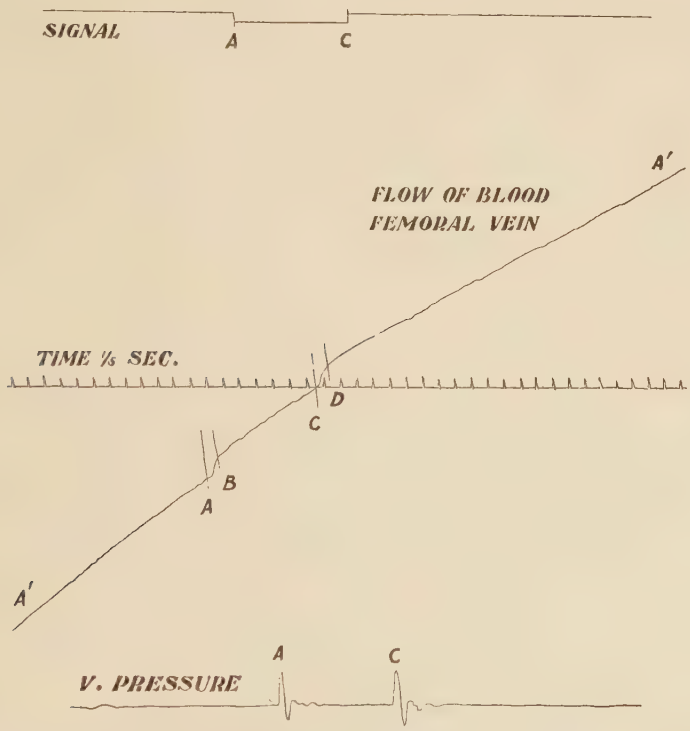

FIGURE 3. — Two-thirds the original size. Variation in venous blood-flow accompanying single muscular twitches (*a*, make, *c*, break of current).

given time. To illustrate: supposing the stromuhr has written three successive phases of the same length. In the first phase only the normal blood-flow is recorded. During the second phase a strong tetanic contraction has been produced, while during the third a single induced current of equal strength and duration has been applied. In

the second case it will be found that the total quantity of blood propelled during the phase is considerably less than the normal volume. The decrease will be the greater, the longer the duration of the tetanization and the stronger the current. Even if the blood-flow is greatly increased by the muscular shortening, the reduction in the blood-volume during the contracted state of the muscle far outweighs the former effect. In the third case, on the other hand, the total quantity will be greater than normal, the increase being proportionate to the volume of blood propelled during the rising periods of the muscular twitches.

The greatest increase in the venous blood-flow is therefore produced by a series of single muscular twitches. The same result can be obtained by successive tetanic contractions, but their duration must be very brief, so that only the quantitative effect of the period of muscular shortening can become evident. If continued for a long time, the retardation of the flow during the tetanic state of the muscle will naturally cause a decided decrease in the total quantity of blood propelled.

Summary.

1. The value of the blood-flow measured in nine dogs varied from 0.50 c.c. per second to 1.20 c.c. per second. The average flow was 0.85 c.c. per second; average weight of dog, 14.2 kilos.

2. The velocity of the blood-stream varied from 48.5 mm. per second to 74.7 mm. per second; average velocity, 61.6 mm. per second.

3. Compression of the femoral artery caused a reduction in the blood-volume of from 63 to 90 per cent; average decrease, 75 per cent.

4. Section of the nerves innervating the posterior extremity was followed by an increase in the blood-volume of from 2.6 to 3.1 times the normal value; average increase, 2.8 times.

5. The variations in the venous blood-flow accompanying a tetanic muscular contraction may be divided into three periods: —

1. Period of great flow, synchronous with the muscular shortening.

2. Period of slight flow, continuing during the contracted state of the muscle.

3. Short period of increased flow, following the relaxation of the muscle.

Differences in the force of the muscular contraction do not alter the

general character of the variation, but only cause changes in the amplitude of its various details.

6. If single induction shocks are used, a great increase in the flow results during the periods of rising energy of the muscle. Between the twitches the blood-flow resumes its normal value.

7. The venous pressure changes during a tetanic contraction in a corresponding manner. There is a quick rise during the muscular shortening and an almost equally rapid fall after the maximal contraction has been reached. During the first part of the tetanization, the pressure remains slightly below normal, while during its latter part the pressure gradually rises and continues slightly above normal for a short time after the relaxation of the muscle.